KALMIOPSIS FRAGRANS (ERICACEAE), A NEW DISTYLOUS SPECIES FROM THE SOUTHERN CASCADE MOUNTAINS OF OREGON

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ABSTRACT

The azalea-like genus *Kalmiopsis* Rehder (Ericaceae) is endemic to southwestern Oregon, U.S.A., and has two disjunct centers of distribution. One is found in the Klamath (Siskiyou) Mountains of Curry and Josephine cos., within the U.S. Forest Service administered Kalmiopsis Wilderness Area. The other is located approximately 150 km northeast in the southern Cascade Mountains of Douglas Co. *Kalmiopsis* is horticulturally significant, and plants from both localities have been established in the garden trade since shortly after their initial discoveries in 1930 and 1954, respectively. The genus has traditionally been considered monotypic, consisting only of *Kalmiopsis leachiana* (Hend.) Rehder. However, comparative studies of the morphology, floral biology, and ecology of the northern and southern population groups have determined they are best treated as distinct taxa. The northern populations are described here as the new species **Kalmiopsis fragrans,** a rare endemic occurring on silicified tuffaceous outcrops within a narrow segment of the Umpqua National Forest.

RESUMEN

El género de azaleas *Kalmiopsis* Rehder (Ericaceae) es endémico del suroeste de Oregón, U.S.A., y tiene dos centros disyuntos de distribución. Uno se encuentra en las montañas Klamath (Siskiyou) de los condados de Curry y Josephine, en la Kalmiopsis Wilderness Area administrada por el U.S. Forest Service. La otra esta localizada a unos 150 km al noreste en el sur de las Cascade Mountains de Douglas Co. *Kalmiopsis* es importante desde el punto de vista de la horticultura, y hay plantas comercializadas de ambas localidades desde poco después de su descubrimiento inicial en 1930 y 1954, respectivamente. El género ha sido considerado tradicionalmente como monotípico, únicamente con *Kalmiopsis leachiana* (Hend.) Rehder. Sin embargo, estudios comparativos de la morfología, biología floral, y ecología de los grupos de poblaciones del norte y del sur han determinado que es mejor tratarlos como taxa distintos. Las poblaciones del norte se describen aquí como la especie nueva **Kalmiopsis fragrans,** una especie endémica que aparece en afloramientos silíceos en una pequeña parte del Umpqua National Forest.

INTRODUCTION

Kalmiopsis Rehder is the only vascular plant genus endemic to the state of Oregon. The interesting circumstances of its discovery are chronicled in Kirkpatrick et al. (1994). Populations were first observed by botanists in 1930 in the mountains of southwestern Oregon (Henderson 1931; Rehder 1932), a rugged area with few trails and limited access. Although this craggy and remote region was already gaining significance as a haven for unusual and relict species (Whittaker 1960), the report of this beautiful, low-growing shrub, reminiscent of *Kalmia* and various cultivated azaleas (*Rhododendron* spp.), attracted considerable taxonomic and horticultural interest (Love 1991). Within months of its discovery, efforts were underway to introduce *Kalmiopsis* to the nursery industry. Although early tradesmen found *Kalmiopsis* a difficult subject for propagation (Love 1991; Kirkpatrick et al. 1994), plants may be grown with perseverance (Mulligan 1973; Kruckeberg 1982) and are today occasionally established in private and public gardens in the Pacific Northwest, Europe, and elsewhere.

Kalmiopsis has a bimodal distribution pattern, occurring most abundantly in the Klamath (Siskiyou) Mountains of Curry and Josephine cos., Oregon, just inland from the Pacific Ocean near the California border. A second, more restricted series of populations is clustered approximately 150 km to the northeast within the Umpqua River watershed of the southern Cascade Mountains, an area with a very different geologic and vegetative history (Whittaker 1960; Marquis 1977). The older Klamath Mountains connect the Coast Ranges

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of Oregon and California, and encompass a complex series of Mesozoic (Jurassic) formations including breccias, tuffs, sandstones, cherts, and conglomerates, much of which has been altered to metavolcanics (Baldwin 1974; Ramp 1975; Marquis 1977). Ultramafic substrates are widespread in the Klamath Mountains, where *Kalmiopsis* populations routinely occur on harsh, open serpentine habitats, though they are not necessarily restricted to them. The geology of the North Umpqua River drainage in the southern Cascades is mostly of Cenozoic origin (Peck et al. 1964), with the handful of *Kalmiopsis* populations here endemic to localized pinnacles of siliceous tuff, mostly in deep coniferous forests.

Henderson (1931) described the newly discovered species as *Rhododendron leachianum*, initially aligning it with the arctic-alpine *R. lapponicum*. Shortly thereafter, Rehder (1932) evaluated the new species and considered it to be closely related to the montane Eurasian genus *Rhodothamnus*, with possible affinities to the circumboreal genera *Kalmia*, *Rhododendron*, and *Phyllodoce*. Rehder ultimately concluded that the Oregon plants were unique enough to merit establishing the monotypic genus *Kalmiopsis*. Copeland (1943, 1954) subsequently placed *Kalmiopsis leachiana* (Hend.) Rehder within *Rhodothamnus*, proposing to drop the new genus based primarily on anatomical similarities between the taxa. However, Davis (1962), in his more recent study of *Rhodothamnus*, disagreed with the assessments by Copeland, and *Kalmiopsis leachiana* remains the currently accepted epithet (Stevens 1971; Harborne and Williams 1973). Recent phylogenetic studies of the subfamilies Rhododendroideae and Phyllodoceae (Kron and King 1996; Kron 1997; Kron et al. 2002) likewise align *Kalmiopsis* with *Rhodothamnus*, supporting the earlier conclusions by Rehder (1932) and Copeland (1943, 1954). However, based on *matK* and *rbcL* sequence data, Kron (1997) and Kron et al. (2002) consider *Kalmiopsis* most closely related to *Phyllodoce*, the genera also being linked by their distinctive multicellular hairs with biseriate stalks.

The discovery of *Kalmiopsis* populations in the Cascade Mountains raised questions about the relationship between these plants and those from the Klamath Mountains to the southwest. Well before taxonomic questions were posed, nurserymen noticed apparent differences between the disjunct populations, recognizing the hardier nature and comparative ease in transplanting of the Cascadian plants (Love 1991). Callan (1971) and Marquis (1977) acknowledged potential morphological differences between the populations as well, implying that recognition as distinct taxa might be warranted. However, neither author proposed any formal taxonomic separation.

In the last few years, opportunities have arisen for more extensive field studies of the genus in the Klamath and Cascade Mountains. The research described here, undertaken to evaluate the suitability of separating the groups as discrete taxa, contrasts the morphology, floral biology, and ecology of the northern and southern populations of *Kalmiopsis*. Herbarium material (including the holotype of *K. leachiana*) and live specimens from eleven populations (four from the Cascades and seven from the Klamath Mountains) were utilized in the comparisons. Measurements were taken from fresh flowers, as many herbarium specimens of *Kalmiopsis* tend to have shriveled corollas that underrepresent floral dimensions. Results from our studies support the recognition of the isolated northern populations as a distinct species.

Kalmiopsis fragrans Meinke & Kaye, sp. nov. (**Figs. 1–4**). Type: U.S.A. OREGON. Douglas Co.: ca. 0.7 km W of Dry Cr. settlement, above N Umpqua R. on S exposure of cliffs along Panther Leap, Umpqua National Forest, T 26S R2E S19 NE ¼, elev. ca. 570 m, in mixed coniferous forest with *Pseudotsuga menziesii, Tsuga heterophylla, Whipplea modesta, Castanopsis chrysophylla, Polystichum munitum,* and *Linnaea borealis, 18 May 1993, R. Meinke and T. Kaye 6280* (holotype: OSC; isotypes: HSC, NY, RSA, UC, US, UTC, WS, WTU).

Plantae ab *Kalmiopsis leachiana* habitu erecto aut serpenti, limbo corollae fisso ad 2–3 mm prope tubum, limbo et tubo corollae fere plano et rotato ubi maturo, ovario luteolo, ciliis densis ad bases filamentorum et in tubo corollae, odore florum simili ad azaleam differt.

Evergreen **shrub**, ± woody below (depending on age and size), usually openly branched (although internodes will shorten and habit become condensed in full sun), mature plants tenaciously rooted in shallow soils on the forest floor, or more often loosely attached and clambering over rocky substrates with thin organic mats, sometimes draped over or hanging from vertical cliffs, occasionally suspended under rock overhangs, capable of vegetative propagation by subterranean stems (often through rock fissures) or via adventitious rooting,

Fig. 1. Flowers of *Kalmiopsis fragrans*, growing in the Limpy Rock Research Natural Area, Umpqua National Forest, Douglas Co., Oregon.

occasionally crown-sprouting, locally forming populations consisting of one or few clones; **stems** few to numerous, (2–)4–12(–30) dm long, ± erect to trailing and occasionally ± matted, arising from a thickened base, glabrous or rarely with sparse, fine, white pubescence, often brittle, exfoliaceous, epidermis reddish to gray, terminally leafy and mostly naked below, the new growth ± stipitate-glandular and often fragrant with a faintly sweet scent; **leaves** numerous, crowded above (or less so in deep shade), thinly coriaceous with a thick cuticle above and below, dark green, glabrous, and shining above (or reddish in anthocyanic individuals in full sun), paler and punctately dotted with golden-crystalline, sweetly aromatic glands below, blade (5)8–30(–45) mm long, elliptic to obovate, apiculate, petioles glabrous to finely puberulent, less than one-fifth the length of the blades, erect to horizontally oriented; **inflorescence** terminal, corymbose to ± racemose, (2–)4–8(–12) per corymb, floral bud scales 2–3 mm long, membranaceous, glabrous or with scattered crystalline glands, pale to reddish-pink, broadly lanceolate; **flowers** dimorphic, consisting of long- and short-styled forms on separate plants, ± aromatic with a spicy-sweet odor, somewhat azalea-like, the aroma persisting and often intensifying with age; **pedicels** 0.5–2.5(–3.3) cm long, mostly glandular-pubescent; **calyx** glabrous, urceolate to campanulate, greenish to mostly pale pink or red, sepals 3–6(–8) mm long, overlapping at the base, thin, broadly lanceolate, margins ± involute; **corolla** pale reddish-purple to deep pink when fresh, deciduous, actinomorphic, lacking a defined throat, the shallow tube <2 mm deep, the limb 16–28(–33) mm across, broadly cupped to campanulate in early anthesis but becoming essentially rotate with age as the petal lobes reflex, lobes deltoid-ovate, 6–12 mm long and 4–8 mm wide, with two parallel, ventral ridges giving petals the appearance of thickness, petal sinuses divided to within 2–3 mm of the corolla tube, the lower edges of the petal lobes overlapping; **stamens** 10, nestled along the petal ridges in

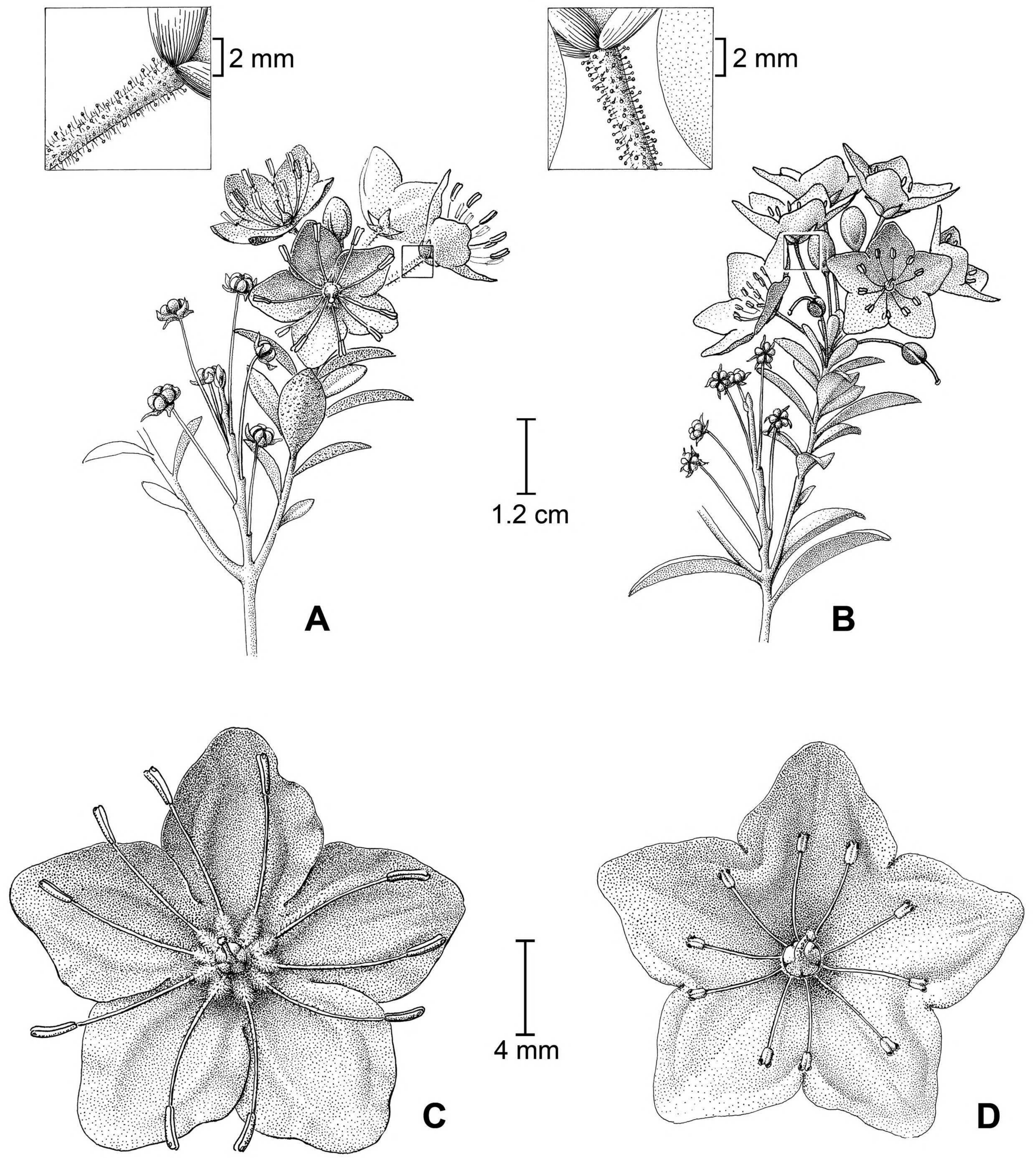

Fig. 2. Inflorescences (with capsules) of *Kalmiopsis fragrans* (A) and *K. leachiana* (B). Insets depict floral stem pubescence – young stems of *K. fragrans* often possess both glandular and non-glandular hairs, while *K. leachiana* is often only glandular, though this trait is variable. Corollas of *K. fragrans* (C) and *K. leachiana* (D) at early anthesis (18–24 hrs after bud break), showing petal sculpturing and stamen positioning.

bud and as corollas open, spreading to erect and well exserted at full anthesis, those of long-styled flowers 7–13 mm long and those of short-styled flowers 11–16 mm long, filaments light pink or paler, basally dilated, glabrous or with scattered hairs above, typically with a copious tuft of pale yellow to golden translucent hairs present at the very base (rarely subglabrous throughout), these joining to form a dense ring of pubescence in the floral tube that surrounds and generally conceals the base of the ovary; **anthers** light purple, narrow-oblong, often slightly curved, 1.2–3.0 mm long, the terminal pore openings <0.4 mm across; **pollen** cream to

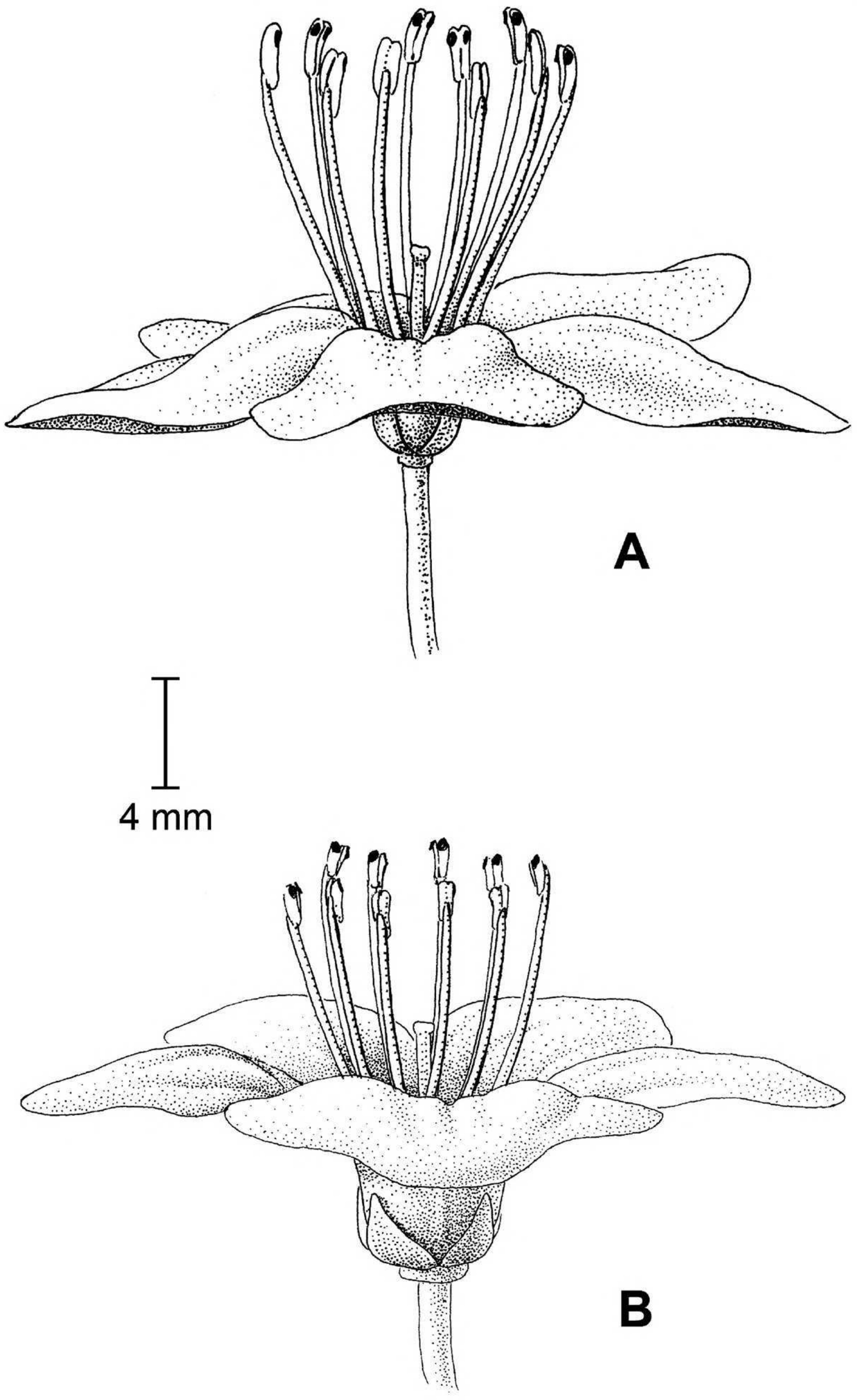

Fig. 3. Flowers of *Kalmiopsis fragrans* (A) and *K. leachiana* (B) at late anthesis (ca. 3–4 days after bud break), showing relative reflexing of petals and change in position (contrast with Fig. 2) of stamens.

ochroleucous, tetrads, 50–60 µ, no differences noted between floral morphs; **styles** red to purple, usually glabrous or rarely with a few isolated hairs, 11–15 mm long in long-styled morphs and 5–8 mm long in short-styled morphs; **stigma** pale, rounded, ± capitate to shallowly bi-lobed, obviously sticky, no differences noted between floral morphs; **ovary** 2–3 mm wide and high, globose, pale yellowish gold, glandular, ovules numerous; **capsule** ± depressed, 3–5 mm broad, shallowly five-lobed, glandular-warty; **seeds** minute, 0.3–0.7 mm long, oblong, shallowly pitted, potentially over 150 per capsule (although abortion may result in far fewer).

Distribution and Habitat.—*Kalmiopsis fragrans* is endemic to a narrow area along the west slope of the southern Cascade Mountains in Douglas Co., Oregon, with a known elevational range of 450 to 1325 m. It is apparently restricted to lands administered by the Umpqua National Forest, mostly within the drainage of the North Umpqua River in the vicinity of Steamboat and along Ragged Ridge. Populations normally occur in deeply shaded to partially open sites, commonly on or closely adjacent to talus slopes, boulder piles, or immense pillars of silicified tuff with south-facing aspects. The new species occurs in mixed coniferous forests variously dominated by *Pseudotsuga menziesii*, *Abies grandis*, *Tsuga heterophylla*, *Calocedrus decurrens*, *Arbutus menziesii*, *Thuja plicata*, and *Pinus lambertiana*. Understory associates include *Berberis nervosa*, *Holodiscus discolor*, *Gaultheria shallon*, *Oxalis oregana*, *Whipplea modesta*, *Castanopsis chrysophylla*, *Polystichum munitum*, *Linnaea borealis*, *Rosa gymnocarpa*, *Pterospora andromedea*, *Pleuricospora fimbriolata*, *Allotropa virgata*, *Rhododendron macrophyllum*, *Acer circinatum*, *Rhus diversiloba*, *Goodyera oblongifolia*, *Thermopsis montana*, *Iris chrysophylla*, *Pyrola picta*, *Sanicula graveolens*, *Viola orbiculata*, *Calypso bulbosa*, *Erythronium citrinum*, and *Luzula campestris*.

Most reproductive individuals and seedling recruitment are found in areas of filtered sunlight on rocky slopes, as well as on rock columns and other semi-moist outcrops that extend into or through the forest canopy. A few populations occur on exposed, rocky ridges. However, *K. fragrans* is a shade-tolerant species, capable of surviving for years within shallow caves and overhangs while growing from high rock ceilings or along deeply sheltered cliffs, persisting in such sites (although with reduced reproductive output) in what are essentially twilight conditions. Populations from deeper forests appear generally intolerant to sudden exposure, and are apt to decline over the long term in response to habitat disturbance that results in reduced soil moisture and increased sunlight. In particular, plants remaining after clear-cuts will persist for a short time, but have been noted to eventually become anthocyanic, more susceptible to disease, and to suffer higher mortality when compared to those from adjacent undisturbed sites.

Flowering.—Populations typically flower from mid-April to early June, depending on elevation. Seed production and dispersal occurs into August. The intensity of flowering in *Kalmiopsis fragrans* appears largely correlated with habitat quality. Plants located in densely shaded conditions may seldom, if ever, bloom or

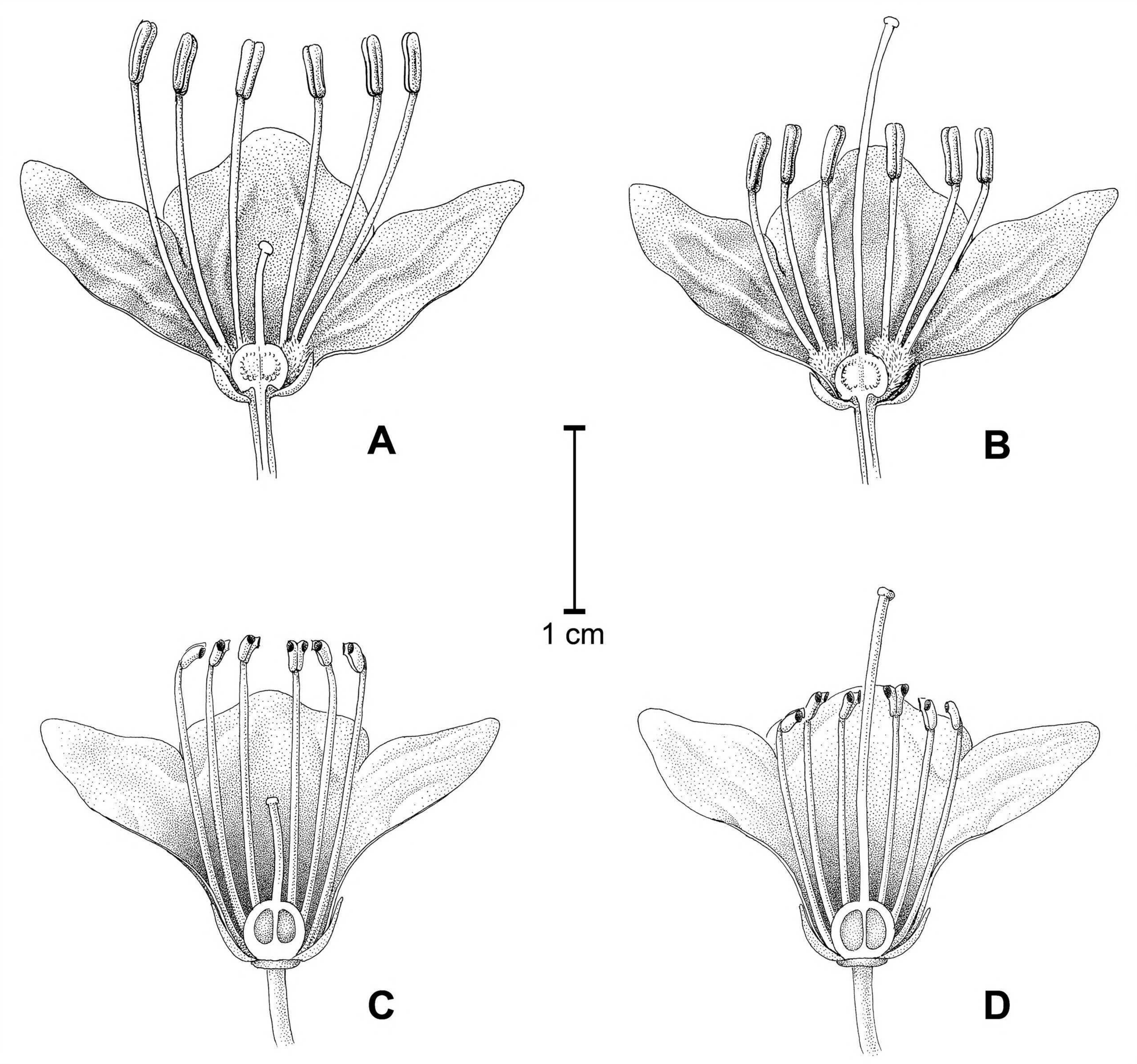

Fig. 4. Cutaway views of short- and long-styled flowers of *Kalmiopsis fragrans* (A and B) and *K. leachiana* (C and D), with details of petal sculpting.

produce seed, while those in areas of consistent, filtered light often flower profusely. Flowering in populations that become highly exposed due to logging or other site disturbance tends to decline over time.

COMPARISON WITH *KALMIOPSIS LEACHIANA*

Overall differences between *Kalmiopsis fragrans* and *K. leachiana* are summarized in Table 1. The floral and inflorescence morphologies of the species are illustrated and contrasted in Figs. 2–4.

Habit.—*Kalmiopsis leachiana* is described as being a small, copiously branched shrub up to 3 dm high (Rehder 1932; Abrams 1951; Peck 1961), but field work associated with this paper indicate that plants of this species may occasionally trail and grow to several dm long on steep terrain. The typical habit, however, is low and compact, with plants often flowering in dense, nearly monospecific stands on hot, barren ridges and open slopes. *Kalmiopsis fragrans*, on the other hand, exhibits marked plasticity in growth form. Plants from the few populations known to occupy exposed ridges may have a habit comparable to *K. leachiana*. However, most individuals are found in forested sites, where they exist as dense, trailing mats on rock outcrops or as loosely erect, openly branched shrubs in the more shaded areas. Plants range from a few dm to nearly

Table 1. Selected morphological, geographic, and habitat characteristics of *Kalmiopsis fragrans* and *K. leachiana*.

Trait	**Kalmiopsis fragrans**	**Kalmiopsis leachiana**
Habit	Erect to trailing or matted	Usually erect
Stem length	To 12 dm, rarely up to 30 dm	2–4 dm, rarely up to 8 dm
Inflorescence size	(2–)4–8(–12) flowers	(5–)7–12(–15) flowers
Corolla size	16–28(–33) mm across	(12–)14–20 mm across
Petal sculpting (best observed on fresh flowers)	Ridges connected within petals	Ridges connected between petals
Petal sinuses	Deeply cleft, to within 2–3 mm of the floral tube	Moderately cleft, to within 4–7 mm of the floral tube
Corolla expansion	Becoming nearly flat and rotate as petal lobes reflex	Petals reflexing but floral tube remaining tubular-cupulate
Corolla color	Light pink or reddish-purple	Rose to deep pink
Style length (long-style)	11–15 mm long	7–10 mm long
Stamen length (long-style)	7–13 mm long	3–7(–9) mm long
Anther size and apical pore dimensions	Narrowly oblong or curved linear, 1.2–3.0 mm, pore ± round, <0.4 mm	Oblong, 0.7–1.8 mm long, pore flared, 0.5–0.9 mm
Ovary color	Pale yellow to gold	Greenish gold
Floral pubescence	Yellowish cilia densely tufted at base of filaments surrounding ovary, evident in floral tube (tube area rarely subglabrous)	Flowers completely glabrous, or occasionally with fine cilia lining basal interior of floral tube, but not tufted or attached to filaments
Floral pollinator attractant	Spicy-sweet "azalea-like" scent and pollen (nectar merely a trace or typically absent)	Nectar pooling in floral tube and pollen (flowers lacking pronounced odor)
Breeding system	Clearly protogynous, pollen shed from a few hours to a day after corolla expansion	Slightly protandrous to slightly protogynous, pollen shed about the time of corolla expansion
Habitat	Mostly on tuffaceous outcrops and within shaded mesic coniferous forest, rooted in rock crevices or in very shallow soil at the base of cliffs or boulders	Plants preferring open sunny ridges, in xeric shrub community or open woodland, in shallow or more often deeper soils on a range of substrates (including ultramafics)
Geographic distribution	Endemic to the southern Cascade Mountains, at elevations ranging from ca. 450–1325 m	Endemic to the Klamath (Siskiyou) Mountains at elevations ranging up to 2100 m

3 m in length, far exceeding the largest examples of *K. leachiana*. Both species are capable of vegetative propagation in nature. This trait is evidently more common in *K. fragrans*, where several populations exceeding 100 individuals are known that appear to consist of one or few clones, based on the presence of only a single floral morph (i.e., long- or short-styled). However, at least two small populations of *K. leachiana* (encompassing <300 m^2) have been reported with only short-styled individuals (Marquis 1977). Moreover, excavations of several apparently separate plants revealed a below ground connection of nearly 2 m in one instance. *Kalmiopsis leachiana* is known to crown sprout after wildfires (Marquis 1977), and *K. fragrans* reportedly may as well (Richard Helliwell, personal communication), although evidence for this was not noted by the authors.

Floral Differences.—Divergence between *K. fragrans* and *K. leachiana* is most apparent in the flowers. The inflorescence of the new species is typically more floriferous (see Figs. 2A and 2B) and the corolla is larger and more deeply cleft than in *K. leachiana* (Figs. 2C and 2D). The proportional differences between the species are evident in corolla width and the size of floral organs, including the anthers, which are nearly twice as long in *K. fragrans* but with much smaller terminal pores. The significance of this is unknown, but the results may include a more prolonged release of pollen in *K. fragrans* (due to the larger anthers and smaller pores)and the deposition of larger pollen loads on individual pollinators in *K. leachiana*. Another interesting feature in *K. fragrans* is the copious pubescence (± golden in nature but pale in dried specimens) often found at the base of the filaments (Figs. 1, 2C), which forms a soft tuft around the base of the ovary. This is all but lacking in *K. leachiana*, a notable exception being the type collection (*Leach and Leach 2915*, ORE), which has some flowers with scattered cilia at the base of the filaments —see Fig. 4 in Rehder (1932). The flower of *K. fragrans* is otherwise subglabrous to glabrous, while *K. leachiana* often exhibits a fine covering of cilia inside the lower corolla tube.

Corollas of both species will remain open up to a week. In the greenhouse, *K. leachiana* flowers may be slightly protandrous or slightly protogynous, with anthers dehiscing at or about the time of initial corolla expansion. The flowers of *K. fragrans* have a more significant female phase, with anthers usually releasing pollen from a few hours to over a day after buds begin to open. Expanded flowers of both species shift from narrowly to broadly campanulate during the first day, with stamens initially splayed out along the corolla away from the receptive stigma (Figs. 2C and 2D). After 1–2 days, stamens become erect and well-exserted (Figs. 3A and 3B), with the filaments encircling the style. The corolla of *K. leachiana* retains a shallow, but well-defined tube that is several mm deep throughout floral ontogeny, with the lobes eventually reflexing perpendicular to the tube (Fig. 3B). The comparatively shallow petal sinuses of *K. leachiana* ensure that the shape of the floral tube remains more or less unchanged even as the lobes reflex, and that it continues to surround the ovary until the corolla drops. Corollas of *K. fragrans* have significantly deeper sinuses, and as flowers age and petal lobes fully reflex the corolla becomes essentially flat and rotate (Fig. 3A), typically exposing the ovary prior to corolla senescence.

Flowers of *K. leachiana* produce a rather viscous nectar (2–10 µL per flower per day in greenhouse plants) and are essentially odorless. Flowers of *K. fragrans* are nectarless, or yield only minute traces, but have a spicy sweet scent that increases in strength after anthers dehisce, and remains evident until corollas are shed. The aroma is especially notable when cut branches are placed indoors, with buds allowed to bloom and age in a confined area. The deeper floral tube of *K. leachiana* serves as a vessel for accumulating nectar, whereas the dense basal ring of stamen hairs in *K. fragrans* may help to delay the dissipation of tiny amounts of nectar or to trap fragrance compounds. Beeflies, syrphid flies, and bumblebees are common visitors to flowers of both species, although foraging patterns differ depending on whether pollen or nectar is being sought. Hummingbirds have also been noted making rapid visits to *K. leachiana* flowers, their foreheads covered in pollen.

Stigma-Height Dimorphism.—*Kalmiopsis* has been described as heterostylous (Callan 1971; Marquis 1977; Love 1991), although the evidence for true heterostyly is circumstantial. *Kalmiopsis* floral morphology (especially *K. fragrans)* is not typical of heterostylous species, which tend to have strongly tubular, campanulate, or funnelform corollas (Ganders 1979). Distyly is otherwise unknown in the Ericaceae, with the possible exception of *Epigaea repens,* a dioecious species that exhibits a continuum of long- and short-styled flowers but lacks other evidence of heterostyly (Darwin 1877; Vuilleumier 1967; Clay and Ellstrand 1981).

While both *K. leachiana* and *K. fragrans* have distinct short- and long-styled floral morphs (Fig. 4), the degree to which the two species also possess the other primary traits that define heterostyly (i.e., reciprocal anther heights and diallelic self-incompatibility – see Ganders 1979) requires further evaluation. Barrett et al. (2000) report that *K. leachiana* flowers clearly are dimorphic with respect to style length, though not for stamens, providing evidence of a stigma-height dimorphism but not necessarily heterostyly (in the sense of intramorph incompatibility). Observations of living and herbarium specimens during this study suggest that reciprocal anther heights may occur in some populations of *K. leachiana*, but this was not confirmed. Conversely, data for *K. fragrans* do show significant reciprocal differences between the floral morphs for both stamen and style lengths (Fig. 5). Field observations of pollinators indicate that this high degree of herkogamy apparently facilitates outcrossing in *K. fragrans*, but is the species functionally heterostylous?

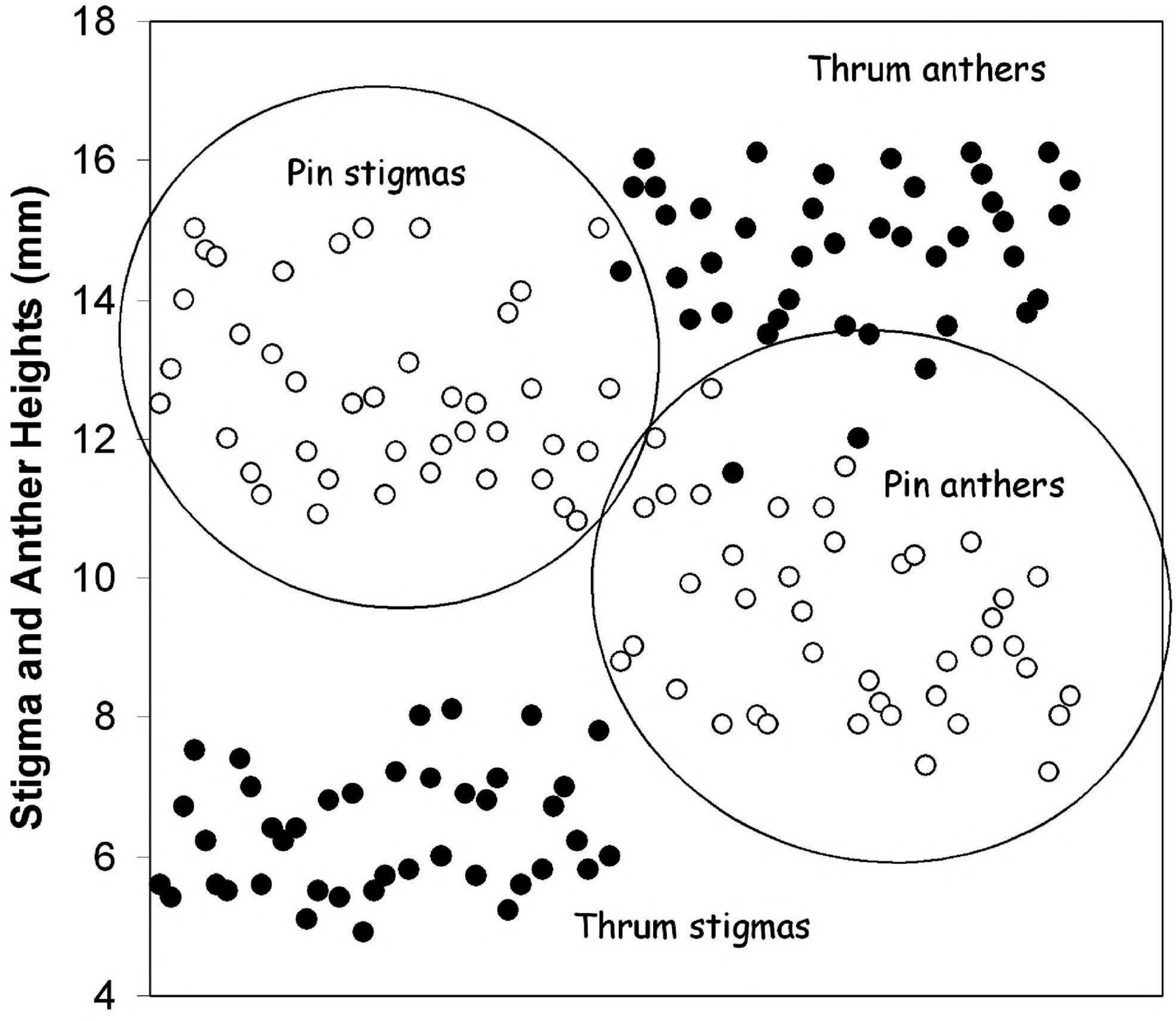

Fig. 5. Spatial relationship between anther and stigma heights for long-styled (pin) and short-styled (thrum) flowers in *Kalmiopsis fragrans* (N=41 for all groups). Data were taken from 24 randomly selected wild plants, 12 for each floral morph (estimated flower age 3–4 days). The mean stamen lengths for pin (9.46 mm) and thrum (14.66 mm) flowers (equivalent to anther height in mature flowers) were significantly different (P<.0001, t=19.266, SE=0.273). Reciprocal herkogamy is a key trait used to define heterostylous species.

Efforts to further evaluate the floral biology of *K. fragrans* through a series of experimental intra- and intermorph pollinations in wild populations were frustrated due to drought. Unseasonably warm, dry weather coincided with sporadic fruit set and a high percentage of abortion among experimental flowers and controls, suggesting that reproduction in our field trials may have been affected by factors other than pollen compatibility. Flowers that were manually selfed, and then bagged, set small numbers of fruit which contained no obvious seeds, but these results may have been similarly skewed by limited rainfall. However, Marquis (1977) also reports evidence for self-incompatibility, albeit in a single greenhouse plant of *K. fragrans*. Although fruit set occurred in 18 out of 28 undisturbed flowers, and in 34 out of 35 flowers self-pollinated by hand, seed production was far below flowers of open-pollinated plants in nature (with an average of less than one seed per capsule in the greenhouse versus 105 seeds from open-pollination). Finally, observations during the current study indicate that fruit set may be depressed or absent within populations consisting of only long- or short-styled ramets, suggesting that self-incompatibility may broadly affect seed production within patches. This was also noted by Marquis (1977). Additional breeding system studies of *Kalmiopsis* are planned.

CONSERVATION STATUS OF *KALMIOPSIS*

Rehder (1932) considered the collection and cultivation of *K. leachiana* essential to its preservation, feeling that the beauty and apparent rarity of the species might eventually lead to its extinction. His concern was evidently justified, as the conservation campaign he advocated quickly attracted the wrong sort of plant enthusiasts.

Commercial collectors almost immediately began to decimate the new species (Love 1991; Kirkpatrick et al. 1994), and entire populations in the Klamath Mountains were wiped out in the 1930's, with one collector reportedly apprehended with 50,000 cuttings on pack horses. Another nurseryman in Portland attempted to raise over 100,000 wild-collected plants for the retail trade (Kirkpatrick et al. 1994), but all died after a single growing season in the wet climate of northern Oregon. Although unbridled commercial collecting was once a legitimate threat to *K. leachiana*, the horticultural novelty of the species has declined and most populations today are considered relatively secure. Moreover, the area in which *K. leachiana* grows is now largely off limits to development due to federal wilderness designation. The species is the namesake for the Kalmiopsis Wilderness Area, a region rich in endemic species and remarkable habitats (Love 1991).

There is no record of *K. fragrans* being mass collected in the wild, and its introduction into the alpine and rock garden trade has evidently been less traumatic. Clones of the species identified as the "LePiniec" form, or occasionally as the "Umpqua River" cultivar (Kruckeberg 1982; Love 1991), are still in cultivation and available today. Recent research at Oregon State University has also demonstrated the relative ease with which *K. fragrans* may be grown from seed (Kelly Amsberry, unpublished).

Of the two species, *K. fragrans* has the narrower geographic range, and it is significantly rarer than *K. leachiana*. Most *K. fragrans* populations are not in designated protected areas, and the species is treated as *sensitive* by the Umpqua National Forest (UNF), a status that affords it more security than most native plants yet less than those formally listed as threatened or endangered. In a few areas the species benefits by sharing its vertical environment with federally-managed peregrine falcons. While frequenting such habitats may shield *K. fragrans* from the effects of timber harvest activity at selected sites, other areas appear less secure. Forest Service staff report that the rocky habitat required by *K. fragrans* is not necessarily a deterrent to either logging or road building, since surveys in advance of both activities have uncovered populations of the new species (Richard Helliwell, personal communication). Fortunately, many populations reside within the Limpy Rock Research Natural Area, which was designated with the preservation of its unique flora in mind. In response to the on-going timber harvest program on the UNF, studies are presently underway to assess how the removal of forest overstory along the edges of tuffaceous outcrops might impact *K. fragrans*.

Representative collections. ***Kalmiopsis fragrans*. U.S.A. OREGON. Douglas Co.:** Limpy Rock, Dog Cr. drainage off the N Umpqua R., 19 Jun 1976, *Chambers 4218* (ORE); same location, 17 May 1975, *Chambers 4041* (OSC); Happy Camp, Umpqua R., Umpqua National Forest, 25 May 1955, *Wright s.n.* (OSC); N Umpqua Hwy., steep hillsides above Horseshoe Bend, on basalt rocks and cliffs, 23 Apr 1967, *Williams s.n.* (ORE). ***Kalmiopsis leachiana*. U.S.A. OREGON. Josephine Co.:** Panther Cr., T37S R9W S6, Siskiyou Mtns., 8 Jul 1950, *Whittaker s.n.* (WS); Kalmiopsis Wilderness, Siskiyou National Forest, T37S R10W S1, 10 May 1997, *Dennis 4838* (OSC); Illinois R., S side of York Peak, 5 May 1957, *Davis s.n.* (OSC). **Curry Co.:** dry rocky spur of Horse Sign Butte, 8 mi S of Agnes, *Applegate 7229* (OSC); Collier Bar, T36S R11W S32, 1–2 May 1931, *Leach 3180* (ORE, WTU, WILLU); the Big Craggy, 19 Jun 1938, *Leach 5247* (OSC); near Game Lake Peak, Siskiyou National Forest, 15 Aug 1938, *Hanson s.n.* (OSC); along Illinois R. Trail, just before the E Fork of York Cr., 24 Apr 1960, *Kezer & Faberge s.n.* (OSC); Siskiyou National Forest, T37S R10W S34, 18 May 1939, *Colville 1* (OSC); Horse Sign Butte, T36S R12W S24, 1 May 1931, *Leach 3179* (OSC, WTU); higher Siskiyou Mtns. of Curry Co. (**holotype**), 14 Jun 1930, *Leach 2915* (ORE).

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